ENVIRONMENTAL INDUCTION OF SHELL MORPHOMETRIC VARIATION IN THE EUROPEAN STREAM LIMPET, *ANCYLUS FLUVIATILIS* (MÜLLER) (PULMONATA: BASOMMATOPHORA)

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ABSTRACT

Specimens of *Ancylus fluviatilis* were collected in the late spring to early summer of 1979, 1982 and 1984 from 25 different freshwater habitats (6 sites sampled in 1982 were again sampled in 1984) in the Republic of Ireland. The shell aperture length (AL), aperture width (AW) and height (SH) of each individual was measured to the nearest 0.1 mm. Shell fractional $CaCO_3$ and protein contents were determined by dissolution of shell mineral components in 12% nitric acid. *A. fluviatilis* has an annual life cycle, allowing mean annual population growth rate to be estimated by dividing the mean AL of the adult generation by its estimated life-span from the approximate date of hatching (30 May). Analysis of variance indicated that significant differences ($P < 0.05$) occurred between the mean shell $CaCO_3$ content, AL/SH, AW/SH and AL/AW of the various populations. AL/SH, AW/SH and AL/AW were allometrically related to AL and AL/AW and AW/SH, allometrically related to annual population growth rate. Population mean AL/SH was not correlated with growth rate due to a significant reduction in the relative AI of individuals from faster growing populations. Population mean shell $CaCO_3$ content, AL/AW, AL/SH and AW/SH were found to vary significantly both in closely adjacent upstream and downstream collections from the same river and over time (1982-1984) in the same population. As shell growth rate in freshwater pulmonates is highly correlated with primary productivity, the majority of interpopulation variation in the shell shape of *A. fluviatilis* appears to result from environmentally induced phenotypic plasticity. While the $CaCO_3$ fraction of total shell weight was not correlated with growth rate, total shell $CaCO_3$ weight increased with increased growth rate suggesting that individuals from more productive habitats allocated greater amounts of assimilated energy to shell production. Shell $CaCO_3$ content also varied significantly both by locality (upstream versus downstream) and through time (1982-1984) within populations. The high degree of environmentally induced interpopulation variation in the shell morphometrics of *A. fluviatilis* suggests that intraspecific interpopulation variation in mollusc shells cannot be assumed *a priori* to result from genetic differences (i.e., the result of adaptation to microenvironments or genetic drift). This result has important implications to the study of molluscan fossil lineages.

Freshwater molluscs exhibit extensive intraspecific, interpopulation variation in their shell morphometrics, growth, reproduction, physiology, life history traits and population bioenergetics (for reviews of interpopulation variation in freshwater molluscs see Russell-Hunter, 1961a, 1961b, 1964, 1978, 1983; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983). The basis for such variation has long been a topic of study. As early as 1939 Diver warned that the vast majority of interpopulation variations in species' morphology, ecology and physiology assumed to result from genetic differences between populations could, after careful examination, prove to be non-genetic, environmentally induced phenotypic plasticity in response to subtle microenvironmental variation. Diver (1939) referred to such non-genetic variation as "ecological plasticity." More recently similar reservations about the adaptive significance of intraspecific interpopulation variation have been expressed in detail by Stearns (1980). While carefully controlled

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laboratory rearing and field reciprocal transfer experiments have provided strong evidence for the development of genetically different "physiological races" in freshwater molluscs, the vast majority of intraspecifc, interpopulation variation appears to have its origins in non-genetic environmental influences on phenotypic plasticity (Russell-Hunter, 1964, 1978; Aldridge, 1983; Burky, 1983; McMahon, 1983). Recently, it was shown that presumed extensive genetic differences between the life history tactics of temporary and permanent pond populations of the basommatophoran snail, *Stagnicola (Lymnaea) elodes* (Say) were almost entirely the result of habitat differences in productivity and ambient temperature (Brown, 1983, 1985a). Similarly, interpopulation morphological variation in freshwater molluscs appears to be much greater than isozyme variation (Hornbach *et al.*, 1980; Palgulayan and Enriquez, 1983), implying that morphometric variation has a strong non-genetic, environmental component.

Two aspects of interpopulation morphological variation claimed to have a partial genetic basis in freshwater molluscs are those of variation in shell $CaCO_3$ content and in the shell morphometric ratios: aperture length:shell height or length; aperture width:shell height; and aperture length: aperture width (Russell-Hunter *et al.*, 1967, 1981; Nickerson, 1972; Hunter, 1975; Durrant, 1975; Sutcliff and Durrant, 1977). These interpopulation variations in shell mineral content and morphology have been considered to be genetically based because they were not correlated with the availability of environmental calcium or because they could not be explained by allometry of shell morphology in relation to differences in mean population shell length. However, other studies have shown that shell $CaCO_3$ can be correlated with a number of environmental variables other than Ca^{+2} concentration (Hunter and Lull, 1977) and that shell morphometric ratios can vary within populations between years (Durrant, 1980) or in individuals drawn at different sites along a continuous river population (Durrant, 1975). Such results argue strongly that environmental influences are the primary cause of shell morphometric variation in freshwater molluscs.

One uninvestigated source of non-genetic, interpopulation phenotypic variation in molluscan shell morphmetrics is the possible allometry between shell form and mineral content in relation to shell growth rate. In a review of the allometric growth of molluscan shells, Vermeij (1980) suggested that while there was a strong possibility that shell biometric variation could result from an allometry with growth rate, the relationship between these two variables had not been systematically examined for any molluscan species.

Considering the extensive interpopulation variation in growth rate reported for freshwater molluscan species and its direct correlation with environmental productivity and temperature (Russell-Hunter, 1961a, 1961b, 1978; Aldridge, 1983; Burky, 1983; McMahon, 1983; and references therein) an allometric relationship between shell morphometry and growth rate could account for a large proportion of the intraspecific, interpopulation shell variation previously considered to be genetic. This paper presents an analysis of the relationship between interpopulation variation in shell growth rate and interpopulation variation in shell $CaCO_3$ content and shell morphometric ratios for 25 populations of the freshwater stream limpet, *Ancylus fluviatilis* (Müller), from the Republic of Ireland. The data are utilized to test the hypothesis that the vast majority of interpopulation shell variation in this species can be explained by non-genetic, phenotypic plasticity in response to microenvironmental variation that affects mean population shell size and shell growth rate, and does not require explanations based on genetic mechanisms such as founder effects, genetic drift, and/or natural selection.

METHODS

Specimens of *Ancylus fluviatilis* were collected from 25 isolated freshwater drainage systems in the Republic of Ireland (Table 1, Fig. 1). The majority of collections were made during June and July, with the exception of collections 43, 44, and 46 (Table 1) which were made in late fall or early spring. The 1979 collections were taken from eight sites throughout Ireland (sites 43-50, Fig. 1). In 1982 and 1984 the remaining collections were focused on sites in northwest Ireland, particularly in the southern portion of County Donegal (Fig. 1, sites 1-40). The 1982 collections were taken from 9 sites in County Donegal. Six of the sites collected in 1982 were recollected in 1984 (sites 3&23R, 6&26R, 7&27R, 8&28R, 9&29R, and 11&31R, Fig. 1 and Table 1) along with an additional eight previously uncollected sites (sites 32-39, Fig. 1 and Table 1). The 1984 collecting sites included upstream and downstream stations on the Glennaddragh River separated by 2 km (sites 30 and 39) and the Croleavy Lough Outlet separated by 0.8 km (sites 31R and 32) both in Southern Donegal (Fig. 1).

With the exception of the two upstream-downstream sites, all collection sites were on drainage systems completely isolated from each other from head waters to marine outlets. Therefore, endemic populations of the highly aquatic *Ancylus fluviatilis* were reproductively isolated, dispersal between populations occurring only passively on birds or water beetle elytra (Russell-Hunter, 1978).

Snails were collected by lifting rocks and other hard surfaced debris gently from the substratum and removing all attached individuals by sliding a scalpel blade under the anterior shell edge. Specimens were immediately fixed in 12% (by volume) neutralized formaldehyde and later transferred to 70% alcohol. Sample size ranged from 16 individuals at site 45 to 247 individuals at site 39 (Table 1).

The shell aperture length (AL, the greatest anterior-posterior distance across the aperture), aperture width (AW, the greatest distance across the aperture 90° to the anterior-posterior axis) and shell height (SH, the greatest vertical distance from the apex of the shell to the plane of the aperture) (Fig. 2) of each individual were measured to the nearest 0.1 mm at 10X with an eyepiece micrometer in a binocular dissecting microscope. SH was measured by moving an individual from a water filled measuring dish up the side of a vertically mounted glass cover slip with a small brush. Water surface tension allowed moistened specimens to adhere to

Table 1. Site number (R designates a 1982 site collected again in 1984), site location, generations in sample (A = previous year's adults, J = that year's juveniles), number of sampled individuals in a generation (n), mean generation aperture length (AL), and standard deviation (s.d.) of AL in populations of the European stream limpet, *Ancylus fluviatilis*, collected in the Republic of Ireland.

Site	Location	County	Date of Collection	Generations in Sample	n	Mean AL (mm)	s.d.
1	Spring, Slieve League Mountain	Donegal	29/6/1982	1981A	31	2.95	±0.44
2	Unnamed stream I, Derrylahan	Donegal	05/7/1982	1981A	47	4.28	±0.45
				1982J	70	1.37	±0.26
3	Unnamed stream I, Cashel	Donegal	13/7/1982	1981A	27	4.46	±0.87
				1982J	95	1.77	±0.46
4	Unnamed stream II, Cashel	Donegal	13/7/1982	1981A	35	4.35	±0.30
				1982J	37	1.67	±0.49
6	Glen River, Straboy	Donegal	05/7/1982	1981A	57	3.93	±0.52
				1982J	25	1.28	±0.17
7	Gannew Brook, Mennacross	Donegal	05/7/1982	1981A	50	4.49	±0.66
				1982J	15	1.37	±0.20
8	Unnamed stream II, Derrylahan	Donegal	06/07/1982	1981A	44	5.36	±0.56
				1982J	68	1.93	±0.44
9	Unnamed stream, Fintragh, Killybegs	Donegal	08/7/1982	1981A	45	4.48	±0.70
				1982J	26	1.60	±0.47
11	Croleavy Lough Outlet, Teelin	Donegal	08/7/1982	1981A	45	4.08	±0.53
				1982J	37	1.78	±0.47
23R	Unnamed stream, Cashel (site 3)	Donegal	29/6/1984	1983A	52	4.22	±0.84
				1984J	94	1.89	±0.52
26R	Glen River-Upstream, Straboy (site 6)	Donegal	03/7/1984	1983A	59	3.84	±0.43
				1984J	2	1.25	±0.70
27R	Gannew Brook, Mennacross (site 7)	Donegal	03/7/1984	1983A	49	4.63	±0.56
				1984J	21	1.60	±0.22
28R	Unnamed stream II, Derrylahan (site 8)	Donegal	30/6/1984	1983A	16	5.64	±0.56
				1984J	21	1.84	±0.54
29R	Unnamed stream, Fintragh, Killybegs (site 9)	Donegal	02/7/1984	1983A	30	4.18	±0.57
				1984J	50	1.58	±0.41
31R	Croleavy Lough Outlet Upstream, Teelin (site 11)	Donegal	03/7/1984	1983a	55	3.72	±0.58
				1984J	46	1.67	±0.32
32	Croleavy Lough Outlet Downstream, Teelin	Donegal	03/7/1984	1983A	45	4.30	±0.56
				1984J	52	1.58	±0.37
33	Owenwee River, Carrick	Donegal	03/7/1984	1983A	8	3.90	±0.68
				1984J	69	2.08	±0.41
34	Lough Inch, Trusky Road, Galway	Galway	27/6/1984	1983A	35	4.05	±0.69
				1984J	1	1.20	—
35	Unnamed stream I, Doonin	Donegal	29/6/1984	1983A	52	4.95	±0.64
				1984J	97	1.70	±0.41
36	Unnamed stream, Cladigh Na g'Caoire	Donegal	29/6/1984	1983A	54	3.94	±0.53
				1984J	43	1.62	±0.37
37	Unnamed stream III, Derrylahan	Donegal	30/6/1984	1983A	43	5.36	±0.65
				1984J	43	1.56	±0.26
38	Unnamed stream II, Doonin	Donegal	30/6/1984	1983A	61	4.51	±0.66
				1984J	19	1.45	±0.26
39	Glennaddragh River, Upstream, Kilcar	Donegal	02/7/1984	1983A	52	4.53	±0.57
				1984J	195	1.99	±0.57
43	Glencullen River, Eniskerry	Dublin	22/11/1978	1978A	188	4.06	±0.70
44	Owen Doher River, Tibradden	Dublin	09/11/1978	1978A	61	3.60	±0.45
45	Little Brosna River, Riverstown	Tipperary	13/6/1979	1978A	15	6.69	±1.13
				1979J	1	1.20	—
46	Unnamed stream, Sherkin Island	Cork	15/3/1979	1978A	29	2.93	±0.73
47	Woodford River, Woodford	Galway	13/6/1979	1978A	35	5.92	±1.21
				1979J	11	1.25	±0.15
48	River Liffey, Lucan	Dublin	09/6/1979	1978A	27	6.48	±1.39
				1979J	73	1.23	±0.32
49	Aille River, Doolin	Clare	14/6/1979	1978A	64	4.11	±0.71
				1979J	2	1.20	±0.00
50	Nore River, Castletown	Offaly	14/6/1979	1978A	44	4.64	±0.91
				1979J	22	1.70	±0.32

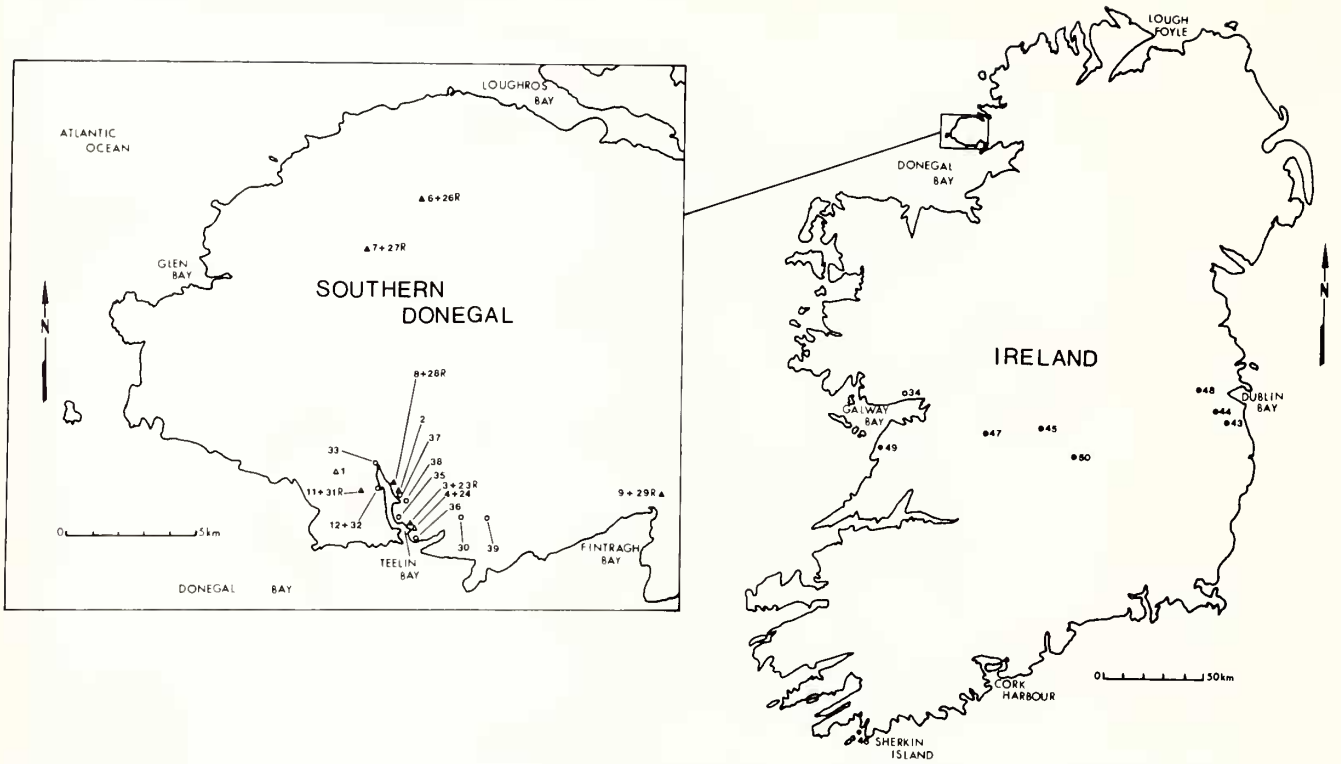

Fig. 1. Map of Ireland showing the locations of collected populations of *Ancylus fluviatilis*. Insert on the left is an expanded portion of the map showing the location of collection sites in southern Co. Donegal. Solid circles indicate populations collected in late 1978 and 1979, open triangles, populations collected in 1982, open circles, populations collected in 1984 and solid triangles populations collected in both 1982 and 1984. Numbers next to collection sites can be used to identify site locations listed in Table 1.

the vertical surface of the cover slip during measurement.

For each sample the number of individuals in each 0.1 millimeter AL size class were expressed as a percentage of the total sample size and plotted as size-frequency polygons in 1 mm intervals (after Russell-Hunter, 1953). Visual examination of these polygons allowed samples to be divided into adult and juvenile size classes. As *Ancylus fluviatilis* is an annual species (Russell-Hunter, 1953; Geldiay, 1956; McMahon, 1980), samples taken in the late spring and early summer were characterized by the presence of two cohorts of individuals marked by distinctly different, non-overlapping distributions of AL. A cohort of larger individuals represented the adults of the previous year's generation and a cohort of smaller individuals represented recently hatched juvenile snails from the oviposition of the previous year's adults (Russell-Hunter, 1953). For Irish populations of *A. fluviatilis* oviposition is initiated in late April to mid-May and hatching occurs approximately two to three weeks later (McMahon, unpublished observations). Similar life cycles have been reported for British populations of this species (Russell-Hunter, 1953; Geldiay, 1956). Therefore, the mean growth rate of the adult generation in each population of *A. fluviatilis* was estimated by dividing the mean AL of that generation by the number of days between an approximate hatching date of 30 May and the subsequent date on which a population was sampled. Multiplying this daily growth rate figure by 30

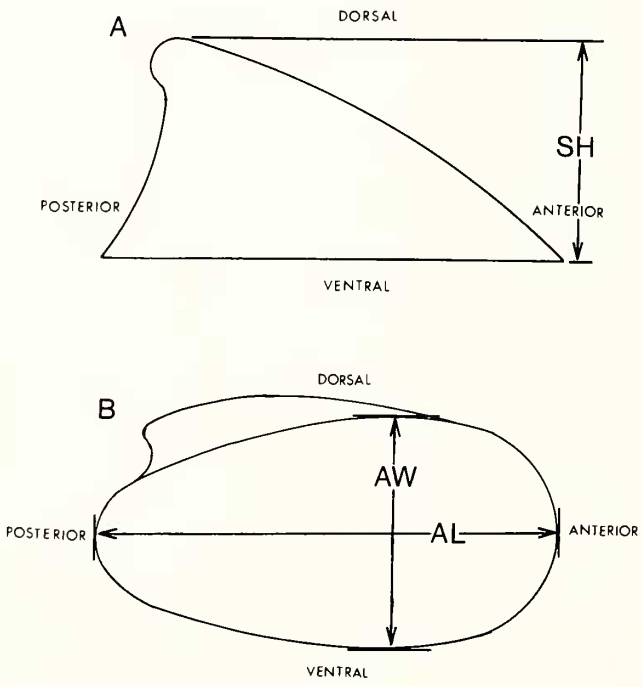

Fig. 2. Linear dimensions measured on the shells of *Ancylus fluviatilis:* AL = aperture length; AW = aperture width; and SH = shell height.

Table 2. Shell morphormetric ratios of Irish populations of the European stream limpet, *Ancylus fluviatilis*, in relation to estimated adult growth rate (mm SL/30 days): Gen. = year of collection and generation (i.e., A is adults of the previous year; J is that year's juveniles); mean shell $CaCO_3$ content = mg shell $CaCO_3$/mg total shell dry weight; AL/AW = mm shell aperture length/mm shell aperture width; AL/SH = mm shell aperture length/mm shell height; and AW/SH = mm shell aperture width/mm shell height. Ratios of AL/AW, AL/SH and AW/SH were estimated for a standard individual with an SL of 4.5 mm from appropriate regressions versus SL for each population (s.e. = standard error).

Site No.	Gen.	mm SL/ 30 days	n	Mean Shell $CaCO_3$ Content (s.e.)	n	AL/AW (s.e.)	AL/SH (s.e.)	AW/SH (s.e.)
1	1981A	0.225	—	———	31	1.38	2.22	1.61
				———		(±0.012)	(±0.064)	(±0.044)
2	1981A	0.321	2	0.937	117	1.27	2.21	1.73
				(±0.005)		(±0.007)	(±0.038)	(±0.033)
3	1981A	0.328	5	0.966	122	1.34	2.10	1.57
				(±0.004)		(±0.008)	(±0.051)	(±0.035)
4	1981A	0.320	4	0.961	72	1.31	2.18	1.66
				(±0.004)		(±0.009)	(±0.043)	(±0.035)
6	1981A	0.295	4	0.903	82	1.32	2.25	1.71
				(±0.005)		(±0.010)	(±0.033)	(±0.025)
7	1981A	0.337	10	0.957	65	1.31	2.11	1.61
				(±0.003)		(±0.008)	(±0.023)	(±0.025)
8	1981A	0.401	4	0.949	112	1.30	2.30	1.77
				(±0.005)		(±0.005)	(±0.025)	(±0.025)
9	1981A	0.334	5	0.963	73	1.32	2.16	1.63
				(±0.004)		(±0.010)	(±0.040)	(±0.035)
11	1981A	0.302	4	0.969	115	1.32	2.16	1.63
				(±0.002)		(±0.008)	(±0.048)	(±0.035)
23R	1983A	0.321	5	0.953	146	1.34	2.07	1.54
				(±0.005)		(±0.008)	(±0.025)	(±0.025)
26R	1983A	0.289	4	0.934	61	1.31	2.24	1.71
				(±0.006)		(±0.010)	(±0.020)	(±0.018)
27R	1983A	0.349	5	0.957	70	1.29	2.21	1.72
				(±0.005)		(±0.006)	(±0.015)	(±0.013)
28R	1983A	0.428	4	0.960	87	1.30	2.30	1.78
				(±0.003)		(0.010)	(±0.045)	(±0.031)
29R	1983A	0.316	5	0.962	80	1.33	2.22	1.67
				(±0.005)		(±0.013)	(±0.030)	(±0.025)
31R	1983A	0.280	5	0.972	101	1.31	2.20	1.67
				(±0.002)		(±0.010)	(±0.033)	(±0.028)
32	1983A	0.324	5	0.981	97	1.30	2.25	1.73
				(±0.003)		(±0.010)	(±0.050)	(±0.038)
33	1983A	0.294	1	0.959	77	1.33	2.26	1.60
				———		(±0.018)	(±0.050)	(±0.044)
34	1983A	0.301	5	0.961	36	1.30	2.17	1.66
				(±0.003)		(±0.007)	(±0.047)	(±0.042)
35	1983A	0.377	4	0.955	149	1.29	2.15	1.67
				(±0.002)		(±0.005)	(±0.025)	(±0.025)
36	1983A	0.300	4	0.948	97	1.30	2.09	1.60
				(±0.004)		(±0.011)	(±0.033)	(±0.025)
37	1983A	0.407	5	0.949	86	1.30	2.19	1.69
				(±0.005)		(±0.008)	(±0.023)	(±0.013)
38	1983A	0.343	5	0.959	80	1.27	2.16	1.69
				(±0.003)		(±0.005)	(±0.015)	(±0.015)
39	1983A	0.342	4	0.934	247	1.30	2.14	1.64
				(±0.006)		(±0.005)	(±0.025)	(±0.018)
43	1978A	0.591	4	0.969	188	1.26	2.15	1.71
				(±0.002)		(±0.003)	(±0.015)	(±0.010)
44	1978A	0.667	3	0.962	61	1.27	2.25	1.76
				(±0.004)		(±0.010)	(±0.035)	(±0.033)
45	1978A	0.531	5	0.956	16	1.30	2.21	1.70
				(±0.003)		(±0.015)	(±0.031)	(±0.026)
46	1978A	0.274	1	0.981	29	1.31	2.21	1.69
				———		(±0.017)	(±0.044)	(±0.042)
47	1978A	0.470	5	0.962	46	1.30	2.37	1.83
				(±0.007)		(±0.010)	(±0.031)	(±0.025)
48	1978A	0.518	5	0.962	100	1.28	2.19	1.72
				(±0.003)		(±0.008)	(±0.018)	(±0.025)
49	1978A	0.325	4	0.959	66	1.29	2.03	1.58
				(±0.004)		(±0.008)	(±0.025)	(±0.019)
50	1978A	0.367	5	0.970	66	1.29	2.23	1.73
				(±0.002)		(±0.008)	(±0.025)	(±0.025)

provided a relatively accurate estimate (± 8%) of mean annual population growth rate in mm AL/30 days. Shell morphometric ratios of AL/AW, AL/SH and AW/SH were then computed for each individual in a population sample. Subsequently, means of these ratios were computed for adult and juvenile cohorts in each collection.

For all samples except that from site 1, shell mineral and organic content of 1-5 subsamples (depending on the number of large individuals in the sample, AL > 3.0 mm) were analyzed by the method of Hunter and Lull (1976). Subsamples for shell component analyses consisted of individuals whose aperture lengths were within ± 0.3 mm of a chosen AL. Subsamples were selected to represent the range of AL in the adult generation of any one sample. The flesh of each individual in a subsample was gently removed from the shell with a pair of fine forceps. The shells were then given two 15 min rinses in distilled water, and subsequently dried to constant weight at 90°C. Thereafter, the mineral ($CaCO_3$) component of each subsample of shells was dissolved in 12% by volume nitric acid. After shell dissolution the remaining organic periostracum and attached organic shell matrix were rinsed three times in distilled water (30 min each for a total of 90 min). The remaining shell organic material was blotted on filter paper and dried to constant weight at 90°C. The weight of the $CaCO_3$ component was estimated by subtracting the dry weight of the remaining shell organic component from total shell dry weight. The shell $CaCO_3$ content of each subsample was expressed as a fraction of total shell dry weight.

RESULTS

Of the 33 collections of *Ancylus fluviatilis,* all but six contained individuals of both adult and juvenile generations (Table 1). Of these six, two consisted only of juveniles spawned that spring (site numbers 30 and 40, Table 1) and four consisted only of the adult generation collected prior to the hatching of juveniles (site numbers 1, 43, 44, and 46, Table 1). The mean shell length of the adult generation in the collections varied by over two fold, ranging from 2.95 mm (site 1) to 6.69 mm (site 45) (Table 1). When 30 May is assigned as an arbitary date for the appearance of a new cohort of juveniles in these *A. fluviatilis* populations (see methods) the annual estimated shell growth rates of adult generations varied nearly three fold from 0.225 mm AL/30 Days (site 1) to 0.667 mm AL/30 Days (site 44) (Table 2). The mean shell growth rate for the adult generation of all collections with the exception of those repeated in 1984 (collections 23R, 26R, 27R, 28R, 29R, and 31R, Table 2) was 0.372 mm AL/30 Days (s.d. = ±0.106, n = 25). Differences between the growth rates of populations collected in 1982 and 1984 were very slight compared to the differences in growth rates between populations (Table 2), suggesting that intrapopulation variation in growth rate is much less than interpopulation growth rate variation. The mean difference in growth rate between populations collected in Donegal in 1982 and in 1984 was 0.015 mm AL/30 Days (s.d. = ±0.008, n = 6, range = 0.006-0.027) or 3.2% of the observed interpopulation variation in shell growth rate across all samples (Table 2).

Least squares linear regression analysis indicated that shell $CaCO_3$ contents were not significantly related ($P > 0.05$) to aperture length both within populations and across all populations (Table 3). Therefore, mean population shell $CaCO_3$ contents were computed from subsample values (Table 2). The mean shell $CaCO_3$ content of subsamples from adult generations (with the exception of site 1 for which collected individuals were too small for accurate shell $CaCO_3$ determinations) varied between 0.903 of total shell dry weight (TSDW) at site 6 and 0.981 of TSDW at site 32 (Table 2). When population differences in mean shell $CaCO_3$ content were analyzed for statistical difference by one-way analysis of variance and a Student-Newman-Keuls Test (Zar, 1974) 124 of 435 or 28.5% of the possible pair-wise comparisons between population means proved to be statistically different at the $P \leq 0.05$ level.

Interpopulation variation in the mean shell morphometric ratios of AL/AW, AL/SH and AW/SH of adult

Table 3. Parameters of least squares linear regressions relating shell $CaCO_3$ content and shell morphometric ratios [Aperture Length to Aperture Width (AL/AW), Aperture Length to Shell Height (AL/SH) and Aperture Width to Shell Height (AW/SH)] to aperture length in mm in all individuals of *Ancylus fluviatilis* taken from 33 collections in Ireland: a = Y intercept; b = slope of the regression line; n = sample size; r = correlation coefficient; F = F statistic; and P = probability level.

Regression Variables	a	b	n	r	F	P
Fraction Shell $CaCO_3$ vs. Aperture Length (mm)	0.946	0.0022	132	0.124	3.04	0.084
AL/AW Ratio vs. Aperture Length (mm)	1.249	0.0113	3506	0.260	254.35	<0.0001*
AL/SH Ratio vs. Aperture Length (mm)	2.467	-0.062	3506	0.378	587.04	<0.0001*
AW/SH Ratio vs. Aperture Length (mm)	1.976	-0.065	3506	0.456	921.80	<0.0001*

*Indicates a significant regression at $P < 0.0001$.

generations were tested with one-way analysis of variance and a Student-Newman-Keuls Test of differences between means. The results of this analysis indicated that all three ratios showed significant interpopulation variation. The AL/AW ratio which is an index of the roundness of the aperture showed the least interpopulation variation. Of 465 possible pair-wise comparisons between population means of AL/AW, 119 or 25.6% were significantly different at $P \leq 0.05$. Both AL/SH and AW/SH ratios, which are indices of steepness of the patelliform shell, showed greater interpopulation variation than did the AL/AW ratio. Of the 465 possible pair-wise comparisons of population mean AL/SH and AW/SH ratios, 148 or 31.8% and 153 or 33.1%, respectively, were significantly different ($P \leq 0.05$).

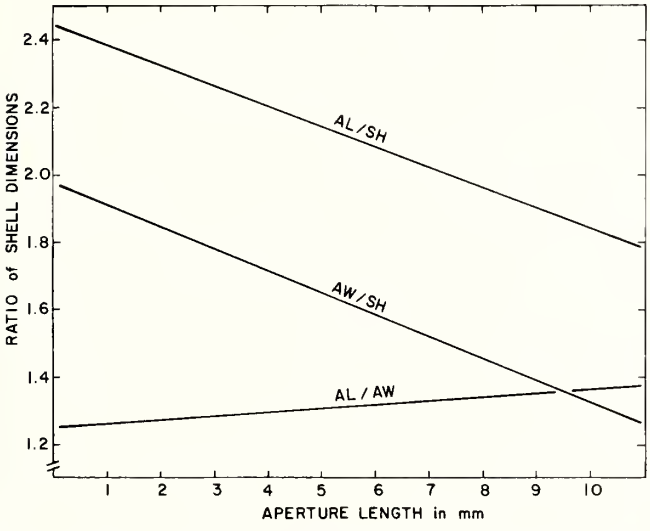

Fig. 3. Allometry of shell morphometric ratios with shell length in all individuals of *Ancylus fluviatilis* collected from 25 populations in Ireland. The y axis is the shell dimension ratios of: aperture length:shell height (AL/SH); aperture width:shell height (AW/SH); and aperture length:aperture width (AL/AW). The solid lines represent best fits of significant ($P < 0.0001$) least squares linear regression equations relating each shell morphometric ratio to shell length in mm (x axis) (see Table 3 for regression parameters.)

Subsequent least squares linear regression analysis indicated that a portion of interpopulation variation in the shell morphometric ratios of *Ancylus fluviatilis* was dependent on shell size, the AL/AW, AL/SH and AW/SH ratios all being significantly correlated ($P \leq 0.05$) with shell size measured as AL within populations. These shell morphometric ratios were also highly correlated with AL ($P \leq 0.0001$) when individual population data were combined across all collections (Table 3, Fig. 3). Regression analysis indicated that the AL/AW ratio increased (the aperture becomes narrower) with increasing AL and that the AL/SH and AW/SH ratios decreased (relative shell elevation increases) with increasing AL (Table 3, Fig. 3). Therefore, the least squares linear regressions relating AL to each of the three morphometric ratios for each individual collection were utilized to predict mean shell morphometric ratios and standard errors for a standard 4.5 mm AL individual from each sample (Table 2). Utilization of a standard sized individual eliminates any bias resulting from differences in adult size distributions of different populations (Table 1) and allows visualization of the allometric relationships not provided by analysis of covariance (Zar, 1974).

Least squares linear regression analysis indicated that the logarithmic transformation of mean population shell $CaCO_3$ content (as % TSDW) was not significantly correlated with the logarithmic transformation of mean population growth rate ($r = 0.135$, $F = 0.519$, $P > 0.5$, $n = 30$) (Table 4). Instead, variation in mean shell $CaCO_3$ content was relatively high between populations with low growth rates (< 0.4 mm AL/30 days) and relatively stable at 96-97% of total shell dry weight in populations with growth rates > 0.4 mm AL/30 Days (Fig. 4).

Least squares linear regressions of shell $CaCO_3$ weight (mg) versus AL for each collection were significant at $P \leq 0.05$. Shell $CaCO_3$ weights of a standard 4.5 mm AL individual estimated from these regressions (with the exception of collections 45 and 48 in which all tested individuals

Table 4. Parameters of least squares linear regressions relating the $\log_{10}$ mean shell $CaCO_3$ content and $\log_{10}$ estimated morphometric ratios of a standard 4.5 mm aperture length individual of *Ancylus fluviatilis* from collections in Ireland to $\log_{10}$ shell growth rate (mm AL/30 Days): AL = aperture length; AW = aperture width; SH = shell height; a = Y axis intercept; b = slope of the regression line; n = sample size; r = correlation coefficient; F = F statistic; and P = probability level.

Regression Variables	a	b	n	r	F	P
Fraction Shell $CaCO_3$ vs. mm AL/30 Days	-0.0149	0.00953	30	0.135	0.519	>0.50
AL/AW Ratio vs. mm AL/30 Days	0.0932	-0.0489	31	0.638	19.881	<0.001*
AL/SH Ratio vs. mm AL/30 Days	0.354	0.0290	31	0.213	1.375	>0.50
AW/SH Ratio vs. mm AL/30 Days	0.264	0.0881	31	0.530	11.329	<0.005*

*Indicates a significant linear regression at $P < 0.005$.

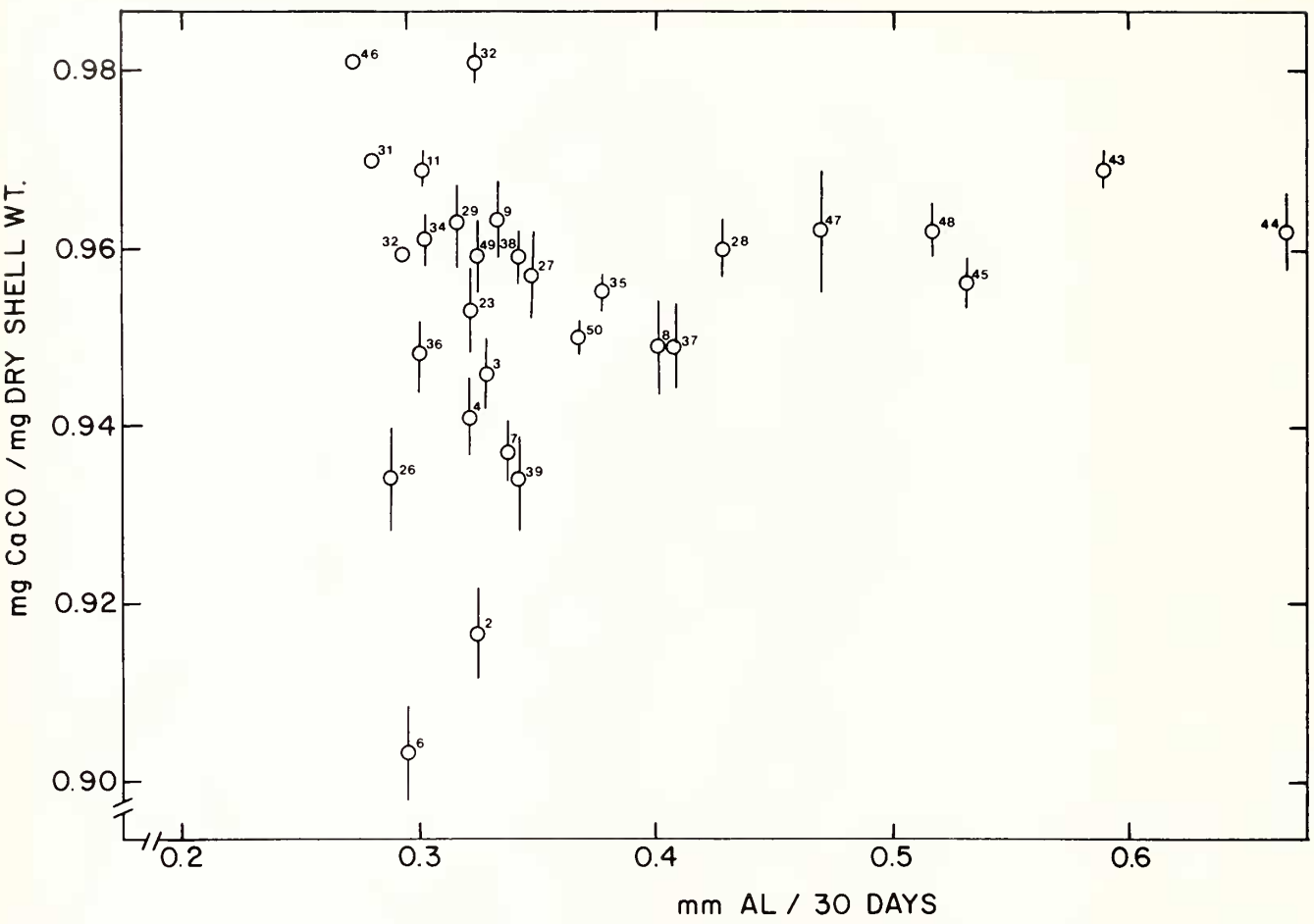

Fig. 4. Interpopulation variation in the population mean shell calcium carbonate content (mg $CaCO_3$/mg total shell weight) (y axis) in relation to annual population shell growth rate in mm aperture length per 30 days (mm AL/30 Days) (x axis) for Irish *Ancylus fluviatilis*. Open circles are mean shell calcium content values of each population for which collection sites are indicated by adjacent numbers (see Tables 1 and 2). Vertical bars are standard errors of the means. No significant correlation ($P > 0.5$) existed between mean population shell calcium carbonate content and growth rate (see Table 4 for regression parameters).

were larger than 4.5 mm Al yielding erroneous estimations of the shell $CaCO_3$ weight of a standard individual) proved to be significantly linearly correlated with annual population growth rate (mm AL/30 days) ($a = 1.55$, $b = 2.98$, $n = 26$, $r = 0.477$, $F = 7.06$, $P < 0.05$) (Fig. 5).

Both the population mean shell AL/AW and AW/SH ratios of a standard 4.5 mm AL individual were significantly ($P < 0.005$) linearly correlated with shell growth rate when ratio and growth rate data were transformed into common logarithms (Table 4). The AL/AW ratio decreased markedly with increasing population shell growth rate ($r = 0.638$, $F = 19.881$, $n = 31$, $P < 0.001$) (Table 4) such that populations characterized by high shell growth rates tended to consist of individuals with rounder shell apertures of greater relative area (Fig. 6). The population mean AW/SH ratio of a standard 4.5 mm AL individual was highly positively correlated with annual population shell growth rate ($r = 0.530$, $F = 11.329$, $n = 31$, $P < 0.005$) (Table 4) such that faster growing populations were characterized by individuals with less elevated patelliform shells (Fig. 7).

Despite the strong linear relationship between the population mean AW/SH ratio and growth rate, the mean population AL/SH ratio was found to be insignificantly linearly related to population mean annual shell growth rate ($r = 0.213$, $F = 1.375$, $n = 31$, $P > 0.5$). Initially this result appeared rather incongruous as the AL/SH ratio, like the AW/SH ratio, is a measure of shell steepness or elevation. It might be presumed that if the AW dimension increases relative to SH in individuals from faster growing populations, then AL should also display a proportionate increase in relation to SH. However, AL decreases relative to AW in individuals from faster growing populations (Fig. 6, Table 4). This decrease in AL relative to AW in individuals from very fast growing populations results in a disproportionate decrease in the AL/SH ratio compared to the AW/SH ratio. Therefore, mean AL/SH ratios of faster growing populations did not increase as population growth rates surpassed 0.5 mm AL/30 days (Fig. 8), resulting in a statistically insignificant relationship

between these two variables (Table 4).

Of two different Co. Donegal river populations of *Ancylus fluviatilis* (Glennaddragh River and Croleavy Lough Outlet) collected at upstream and downstream locations, significant variation occurred in the mean shell $CaCO_3$ content of individuals of approximately the same range of SL between adult generations of the upstream (site 31R) and downstream Croleavy Lough Outlet collections (site 32). The mean shell $CaCO_3$ content of individuals from the downstream site (mean $CaCO_3$ content = 0.981) proved significantly greater than that of those from the upstream site (mean $CaCO_3$ content = 0.972) when tested by a Student's t-test ($P < 0.05$) (Zar, 1974) (Table 5).

Significant differences also occurred between the means of all three morphmetric ratios of the 1984 juvenile generations collected at upstream and downstream sites on the Glennaddragh River (Table 5). Comparisons of shell morphometrics of adult individuals could not be made for the Glennaddragh River as adults were not present in the upstream population sample (site 30) (Table 1). Students t-tests indicated that the mean AL/AW ratio was significantly lower and the mean AL/SH , and AW/SH ratios significantly higher ($P < 0.05$) in individuals collected from the upstream site on the Glennaddragh River (site 39) compared to corresponding mean ratios for individuals taken from the downstream site (site 30) (Table 5). As such, individuals from the upstream site had taller shells with narrower apertures than downstream individuals. No significant differences were observed in the shell morphometrics of upstream and downstream collections ($P > 0.5$) in Croleavy Lough Outlet (Table 5).

Student's t-test also revealed significant differences between the mean shell $CaCO_3$ contents and shell morphometric ratios of populations of *Ancylus fluviatilus* collected at the same sites in different years. Of the six populations for which collections were repeated, the mean shell $CaCO_3$ contents of three populations differed significantly ($P < 0.05$) between 1982 and 1984. Mean shell $CaCO_3$ content was greater in adult limpets taken in 1982 (collection 3) than in those taken in 1984 (collection 23R) from the same site in an unnamed stream in Cashel, Co. Donegal, while the mean shell $CaCO_3$ contents of individuals taken in 1982 at both the Glen River, Straboy, Co. Donegal (collection 6) and an unnamed stream in Derrylahan, Co. Donegal (collection 8) were significantly less than those of adults taken at the same sites in 1984 (collections 26R and 28R, respectively) (Table 6). In all cases the differences in mean SL and growth rate of these populations between 1982 and 1984 were negligible (Tables 1 and 2), thus, allometries of shell $CaCO_3$ content or weight could not account for these morphometric differences in shell mineral content.

Of the six recollected populations, a significant dif-

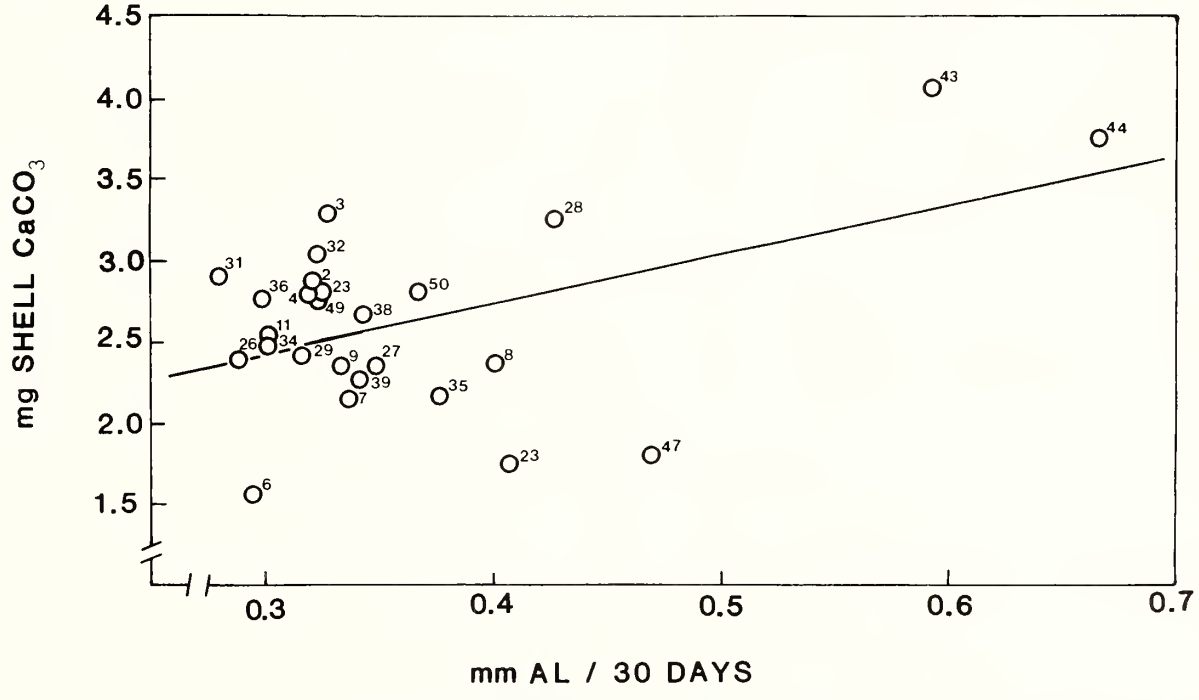

Fig. 5. Allometry of estimated population shell $CaCO_3$ weight (mg) of a standard 4.5 mm AL individual in relation to estimated annual shell growth rate in Irish *Ancylus fluviatilis*. The y axis is mg shell $CaCO_3$ weight estimated for a standard individual from least squares linear regression equations relating mg shell $CaCO_3$ weight to aperture length for each population sampled. The x axis is annual population shell growth rate in mm aperture length per 30 days (mm AL/30 Days). Open circles are the estimated shell $CaCO_3$ weights of a standard 4.5 mm AL individual for each population as indicated by adjacent collection numbers (see Tables 1 and 2). Standard errors about each estimate were smaller than point diameter in all cases. The solid line represents the best fit of a significant least squares linear regression as follows: Shell $CaCO_3$ weight (mg) = 1.55 + 2.98 (mm AL/30 Days) ($r = 0.477$, $n = 26$, $F = 7.06$, $P < 0.001$).

Table 5. Comparison of means of shell $CaCO_3$ content and shell morphometric ratios of aperture length to aperture width (AL/AW), aperture length to shell height (AL/SH) and aperture width to shell height (AW/SH) for Irish populations of *Ancylus fluviatilis* collected at upstream and downstream sites in the same river systems in 1984; n = sample size; s.e. = standard error; and t = t-value.

			Shell $CaCO_3$ Content				Shell Morphometrics								
Site	Site No.	Gen.	$\frac{CaCO_3}{TSW}$	n	s.e.	t-value	n	Mean AL/AW	s.e.	t-value	Mean AL/SH	s.e.	t-value	Mean AW/SH	s.e.	t-value
Glennaddragh River, Upstream	39	1984J	———	—	———	———	195	1.257	±0.005	2.38*	2.316	±0.012	3.91*	1.847	±0.012	4.94*
Glenraddragh River, Downstream	30	1984J	———	—	———	———	129	1.276	±0.016		2.237	±0.016		1.757	±0.014	
Croleavy Lough Outlet, Upstream	31	1983A	0.972	5	±0.002	2.24*	55	1.306	±0.006	0.52	1.726	±0.016	0.52	2.252	±0.020	0.17
Croleavy Lough Outlet, Downstream	32	1983A	0.981	5	±0.003		45	0.301	±0.006		1.736	±0.018		2.257	±0.022	

*Indicates t-values associated with a $P < 0.05$ significant difference between means.

Table 6. Comparison of means of shell $CaCO_3$ content and shell morphometric ratios of aperture length to aperture width (AL/AW), aperture length to shell height (AL/SH) and aperture width to shell height (AW/SL) for Irish populations of *Ancylus fluviatilis* collected in 1982 and recollected in 1984; n = sample size; s.e. = standard error; and t = t value.

		Shell $CaCO_3$ Content				Shell Morphometrics								
Site No.	Date	Mean mg $CaCO_3$/TSW	s.e.	n	t	n	Mean AL/AW	s.e.	t	Mean AL/SH	s.e.	t	Mean AW/SH	s.e.	t
3	13/07/82	0.966	±0.004	5	1.94*	27	1.333	±0.010	0.02	2.062	±0.021	0.28	1.549	±0.020	0.30
23R	29/06/84	0.953	±0.005	5		52	1.333	±0.008		2.053	±0.021		1.541	±0.015	
6	5/07/82	0.903	±0.005	4	3.91**	57	1.316	±0.006	0.46	2.247	±0.014	0.81	1.711	±0.015	0.73
26R	3/07/84	0.934	±0.006	4		59	1.324	±0.017		2.230	±0.016		1.694	±0.018	
7	5/07/82	0.957	±0.003	10	0.04	50	1.328	±0.012	3.08***	2.098	±0.014	15.26***	1.583	±0.013	7.52***
27R	30/06/84	0.957	±0.005	5		49	1.287	±0.005		2.199	±0.013		1.709	±0.011	
8	5/07/82	0.949	±0.005	4	1.83*	44	1.310	±0.009	0.35	2.233	±0.026	0.21	1.709	±0.024	0.08
28R	30/06/84	0.960	±0.003	4		16	1.304	±0.007		2.233	±0.023		1.705	±0.020	
9	8/07/82	0.963	±0.004	5	0.01	45	1.323	±0.007	0.023	2.150	±0.022	1.85*	1.626	±0.017	1.88*
29R	2/07/82	0.962	±0.005	5		30	1.321	±0.009		2.208	±0.021		1.673	±0.016	
11	10/07/82	0.969	±0.002	4	1.08	45	1.317	±0.006	1.37	2.184	±0.015	2.65**	1.660	±0.013	3.16**
31R	3/07/84	0.972	±0.002	5		55	1.306	±0.006		2.252	±0.020		1.726	±0.016	

*Indicates a significant difference between annual collections at $P < 0.05$.
**Indicates a significant difference between annual collections at $P < 0.01$.
***Indicates a significant difference between annual collections at $P < 0.001$.

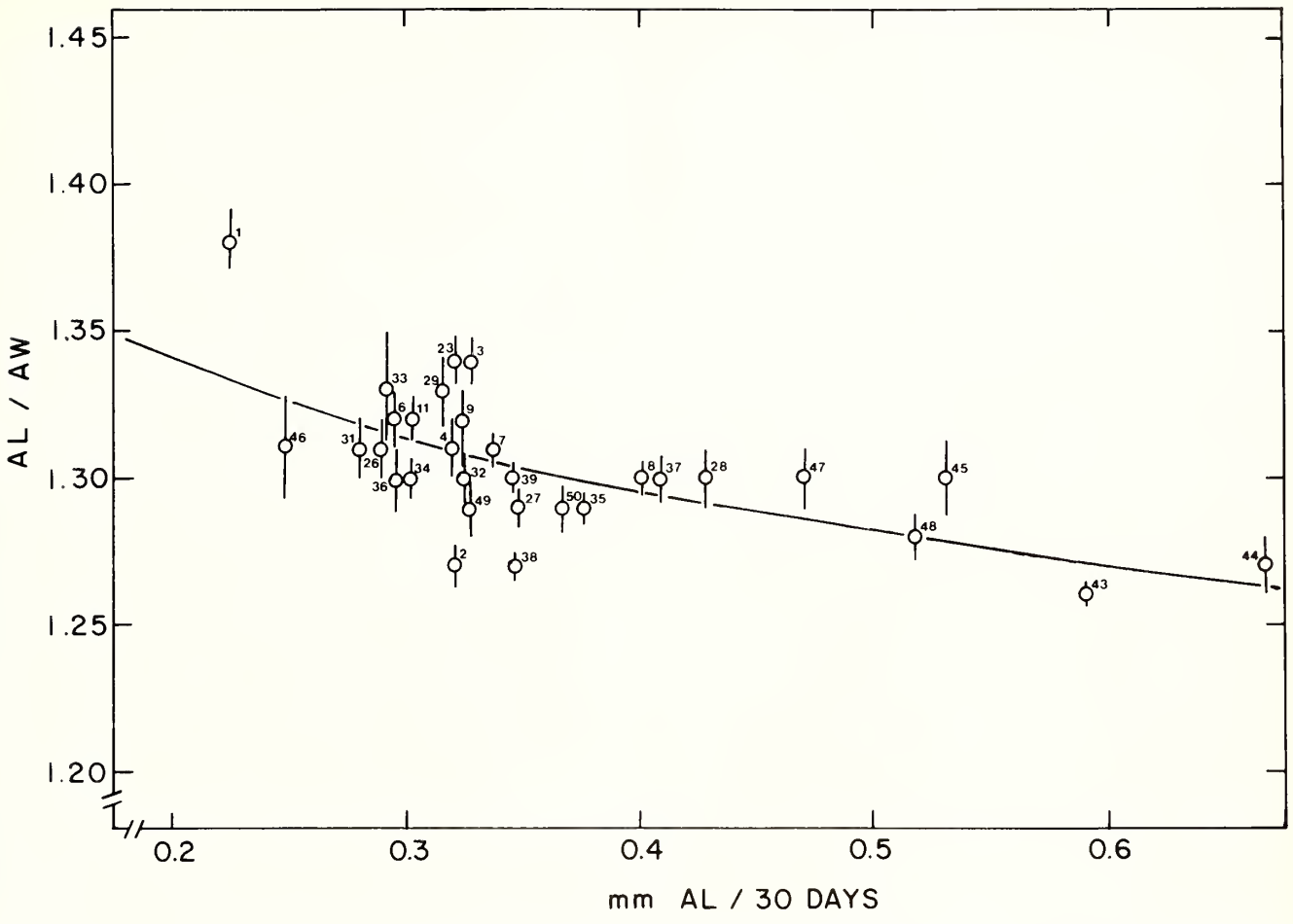

Fig. 6. Allometry of estimated population mean shell length:aperture width ratios (AL/AW) with mean annual population growth rate in Irish *Ancylus fluviatilis* populations. The y axis is the mean shell AL/AW ratio estimated for a 4.5 mm AL standard individual from least squares linear regression equations relating AL/AW to AL for each population collected. The x axis is annual population growth rate in mm AL per 30 days. The open circles are the estimated AL/AW ratio for each population for which collection sites are indicated by the adjacent numbers (see Tables 1 and 2). The vertical bars are standard errors of the means. The solid line represents the best fit of a significant ($P < 0.001$) log-log least squares linear regression equation relating estimated AL/AW to annual population growth rate (see Table 4 for regression parameters).

ference in mean AL/AW ratio of the 1982 and 1984 adult generations was observed only in the Gannew Brook population, Co. Donegal (sites 7 and 27R, Table 6). In this population the mean AL/AW ratio was significantly greater in 1982 (mean AL/AW = 1.328) than in 1984 (mean AL/AW = 1.287) (Table 6). The mean AL/SH and AW/SH ratios of individuals from this population were also significantly greater in 1984 (1982: mean AL/SH = 2.098; AW/SH = 1.583, 1984: mean AL/SH = 2.199, AW/SH = 1.709), indicating that they had less elevated shells with rounder apertures than those taken in 1982 (Table 6). Similar significant increases in the mean AL/SH and AW/SH ratios of adult limpets were also recorded for two other populations in 1984. The mean AL/SH and AW/SH ratios of adult individuals from an unnamed stream in Fintragh, Killybegs, Co. Donegal, were 2.208 and 1.673, respectively, in 1984 (collection 29R), while these values were 2.150 and 1.626 for adults taken in 1982 (collection 9). Similarly, the mean AL/SH and AW/SH ratios of adults taken in 1984 at Croleavy Lough Outlet, Upstream, Co. Donegal (collection 31R) were 2.252 and 1.726, respectively, while those of adults taken there in 1982 (collection 11) were significantly lower at 2.184 and 1.660 (Table 6). None of the significant differences in mean AL/AW, AL/SH and AW/SH ratios observed in populations collected both in 1982 and 1984 could be attributed to allometries associated with changes in mean SL or growth rate between years of collection, as these parameters for the 1981A and 1983A generations at each of these three sites were essentially the same prior to the 1982 and 1984 collections (Tables 1, 2).

DISCUSSION

Russell-Hunter *et al.* (1981) suggest that freshwater molluscs can display four different relationships between shell $CaCO_3$ content and habitat water calcium concentration.

These are: 1. a direct relationship between cell calcium and water Ca^{+2} concentration; 2. regulation of shell $CaCO_3$ content at relatively constant levels over a wide range of environmental Ca^{+2} concentrations; 3. a relation between shell $CaCO_3$ content and trophic conditions (environmental productivity); and 4. great interpopulation variation, but limited intrapopulation variation in shell $CaCO_3$ content reflecting a random geographical distribution of genetic races resulting from founder effects and genetic drift with no obvious adaptive relationship to biotic or abiotic environmental parameters.

Type 1 shell calcium variation is displayed by *Lymnaea peregra* (Müller) (Young, 1975; Russell-Hunter *et al.*, 1981), *Planorbarius corneus* (L.) (Young, 1975), *Biomphalaria pfeifferi* (Krauss) (Harrison *et al.*, 1970), *B. glabrata* (Say) (Thomas *et al.*, 1974), *Cincinnatia cincinnatiensis* (Antony), and a number of sphaeriid and unionid bivalve species (Mackie and Flippance, 1983). Type 2 variation occurs in *Physella gyrina* (Lea) (Hunter and Lull, 1977). Type 3 shell $CaCO_3$ variation occurs in *Helisoma anceps* (Menke) and *Physella integra* (Haldeman) (Hunter and Lull, 1977). Type 4 variation has been reported for *Stagnicola elodes* (Hunter, 1975). A fifth pattern of interpopulation shell variation whereby shell $CaCO_3$ content is inversely proportional to ambient water Ca^{+2} concentration has recently been reported for the sphaeriid bivalves, *Sphaerium simile* (Say), *S. rhomboideum* (Say) (Mackie and Flippance, 1983) and *S. striatinum* (Lamarck) (Burky *et al.*, 1979).

Among ancylid species, the North American stream limpet, *Ferrissia rivularis* (Say), is reported to have a type 4 pattern of interpopulation shell $CaCO_3$ variation. Shell $CaCO_3$ content and organic content (measured in terms of total organic carbon and nitrogen) varied significantly between 10 populations in upstate New York and were neither correlated with each other or with water hardness and dissolved calcium. It was suggested that the synthesis of these two components in this species is under independent genetic controls and that intrapopulation variations in shell $CaCO_3$ and organic contents resulted primarily from differences in the gene pools

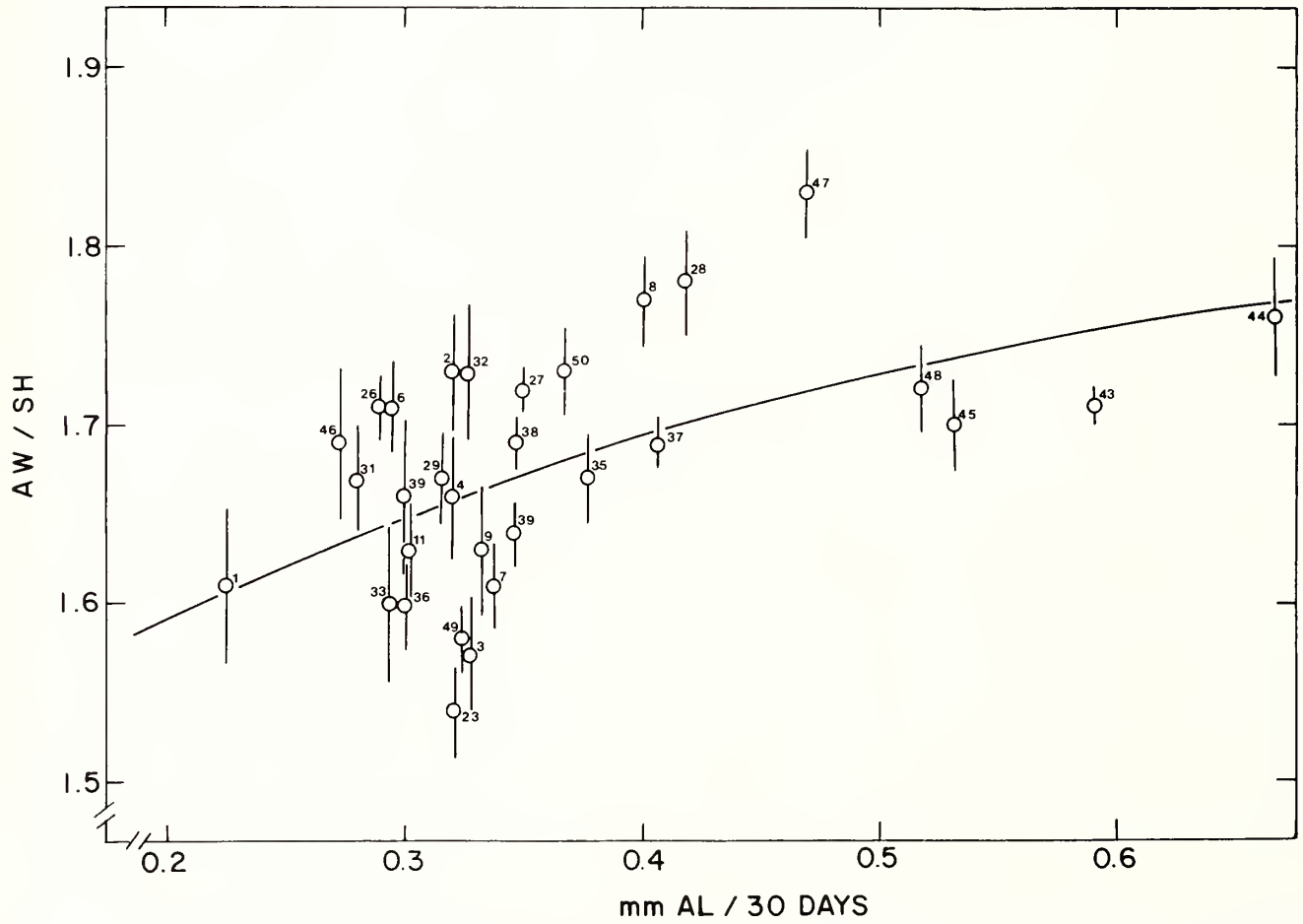

Fig. 7. Allometry of estimated population mean shell aperture width:shell height ratios (AW/SH) with mean annual growth rate in Irish *Ancylus fluviatilis* populations. The y axis is mean shell AW/SH ratio estimated for a 4.5 mm AL standard individual from least squares linear regression equations relating AW/SH to AL for each population collected. The x axis is growth rate in mm AL per 30 days. The open circles are the estimated mean AL/AW ratio for each population for which collection sites are indicated by the adjacent numbers (see Tables 1 and 2). The vertical bars are standard errors of the means. The solid line represents the best fit of a significant ($P < 0.005$) log-log least squares linear regression equation relating estimated AW/SH to annual population growth rate (see Table 4 for regression parameters).

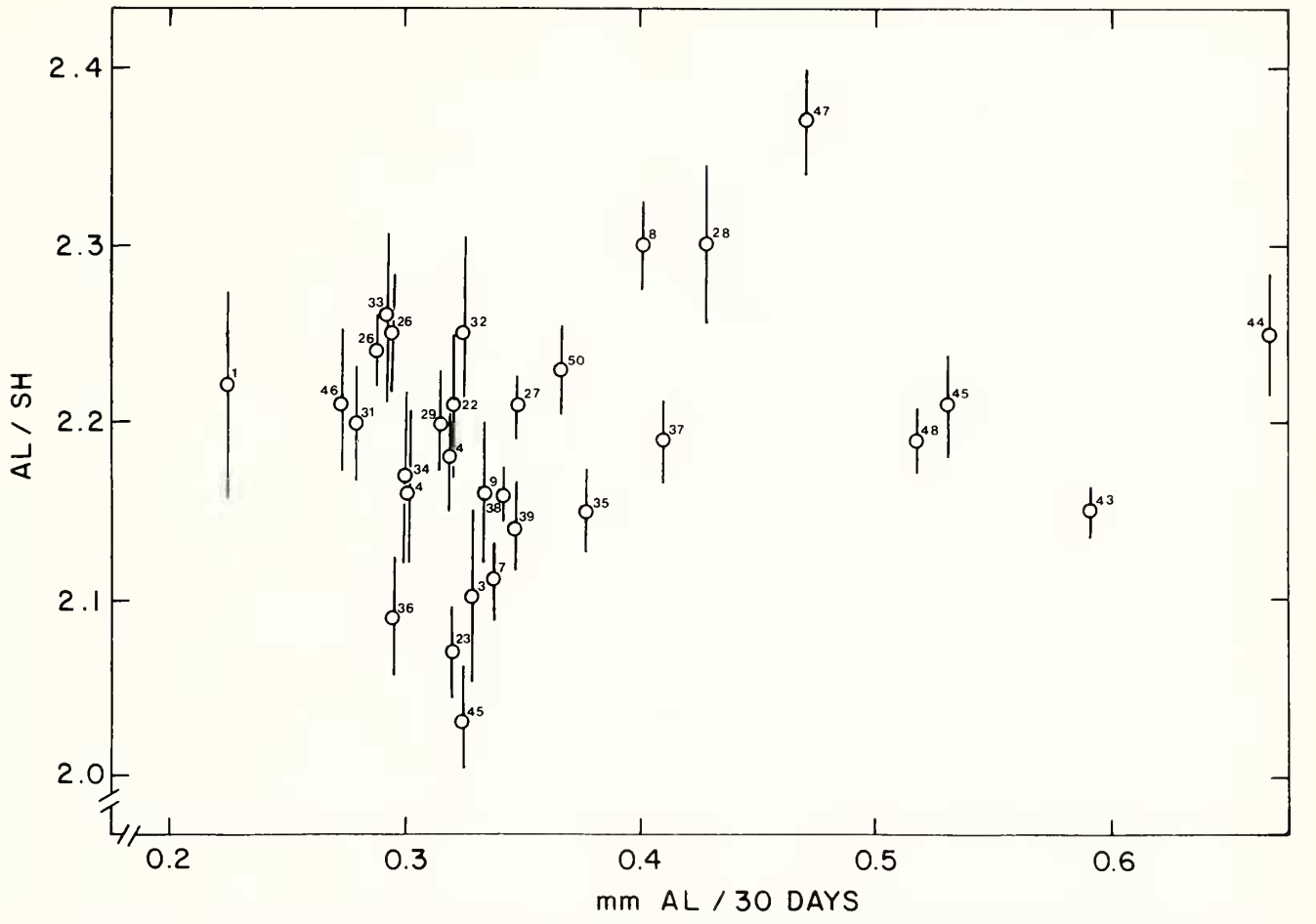

Fig. 8. Interpopulation variation of estimated mean shell aperture length:shell height ratios (AL/SH) in relation to growth rate in Irish *Ancylus fluviatilis*. The y axis is mean shell AL/SH ratio estimated for a 4.5 mm AL standard individual from least squares linear regression equations relating AL/SH to AL for each population collected. The x axis is annual population growth rate in mm AL per 30 days. The open circles are estimated mean AL/SH ratios for each population for which collection sites are indicated by the adjacent numbers (see Tables 1 and 2). Vertical bars are standard errors of the means. There was no significant correlation ($P > 0.05$) between estimated AL/SH ratios and growth rate due to an allometric reduction of AL in relation to AW in faster growing populations (see Results for details and Table 4 for regression parameters).

of reproductively isolated populations (Russell-Hunter *et al.*, 1967, 1981; Nickerson, 1972). In contrast, a direct relationship was found between water Ca^{+2} concentrations and shell $CaCO_3$ content in three populations of the North American pond limpet, *Laevapex fuscus* (C. B. Adams) (McMahon, 1975), indicating that as environmental calcium availability increased so did the amount deposited in the shell. Indeed, such major differences in the patterns of shell $CaCO_3$ content between closely related species occurs more often than not in freshwater molluscs (Burky *et al.*, 1979; Mackie and Flippance, 1983; McMahon, 1983). Differences in the pattern of shell $CaCO_3$ content with ambient Ca^{+2} concentration are even reported between populations of the same species from different geographical areas. Burky *et al.* (1979) report an inverse relationship between shell $CaCO_3$ and environmental Ca^{+2} concentration in populations of *Sphaerium striatinum* from the states of Ohio and New York while Mackie and Flippance (1983) report no correlation between shell $CaCO_3$ and Ca^{+2} concentration for populations of the same species collected in southern Ontario, Canada. Such large variations in the patterns of interpopulation variation of shell $CaCO_3$ content in relation to environmental Ca^{+2} within and between closely related species strongly suggest that abiotic and biotic environmental factors other than Ca^{+2} concentration are acting to induce non-genetic, interpopulation phenotypic plasticity in the shell $CaCO_3$ content of freshwater molluscs.

McMahon (1983) has suggested that interpopulation differences in shell $CaCO_3$ content may be more related to differences in growth rates than to differences in abiotic factors, giving rise to an apparently random (non-adaptive) distribution of interpopulation variation in shell mineral content. In this model faster growing individuals more rapidly expand the mantle edge, and therefore, deposit $CaCO_3$ at the shell edge at a higher rate than slower growing individuals. If deposition of new $CaCO_3$ by the underlying mantle to

thicken the shell occurs at relatively the same rate in slow and fast growing individuals, then shells of more slowly growing individuals will be thicker and have proportionately greater $CaCO_3$ contents (an increased fraction of total shell weight will be accounted for by $CaCO_3$). In both *Laevapex fuscus* and *Stagnicola elodes* shell $CaCO_3$ content was inversely correlated with population growth rate (McMahon, 1975; Hunter, 1975). In addition, shell $CaCO_3$ content in both *Physella integra* and *Helisoma anceps* in 7 sympatric populations was shown to be inversely related to habitat primary productivity (Hunter and Lull, 1977). As growth rates in freshwater pulmonates are directly related to environmental productivity (Russell-Hunter, 1964, 1978; McMahon, 1983; McMahon *et al.*, 1974) the decrease in shell $CaCO_3$ content of populations of these two species from more eutrophic waters may be a direct result of increased population growth rates.

Data from this study of *Ancylus fluviatilis* do not support the above hypothesis. No significant correlations could be detected between the fraction of shell $CaCO_3$ and either the estimated population growth rate or size measured as AL. As such, it appears that interpopulation variation in the the shell $CaCO_3$ content in *A. fluviatilis* was not influenced by size, growth rate or, by inference, environmetnal primary productivity. At first, such a result would seem to argue strongly that, as suggested for *Ferrissia rivularis* (Russell-Hunter *et al.*, 1967, 1981; Nickerson, 1972), shell $CaCO_3$ content in *A. fluviatilus* is under relatively rigid genetic control, with observed interpopulation variation the result of gene pool differences between reproductively isolated populations. However, significant differences in shell $CaCO_3$ content were recorded between individuals collected from upstream and downstream sites in 1 of 2 continuous river populations (Table 5) and between individuals taken from the same site in 1982 and 1984 in three of six collected populations (Table 6). Such extensive variations in shell $CaCO_3$ contents at different points in continuous populations and over a time span of only two years the same populations almost certainly resulted from environmental influences operating on phenotypic expression ("ecological plasticity", see Diver, 1939; Stearns, 1980) rather than from genotypic differences due to founder effects, genetic drift or natural selection.

The basis for such environmentally induced variation in shell $CaCO_3$ content remains unclear. However, there is recent evidence that a number of other environmental factors can have greater effect on shell $CaCO_3$ content of freshwater molluscs than either growth rate or ambient Ca^{+2} concentration. Increased current flow has been shown to be correlated with increased shell weight in pisidiid clams (Bailey *et al.*, 1983). Mackie and Flippance (1983) demonstrated that in 11 of 28 species of freshwater molluscs shell $CaCO_3$ mass was correlated with ambient pH, including three gastropod species [*Gyraulus parvus* (Say), *Cincinnatia cincinnatiensis* and *Valvata tricarinata* (Say)]. In only one gastropod species, *C. cincinnatiensis*, was shell $CaCO_3$ mass directly related to water Ca^{+2} concentration while it was related to total hardness in both *G. parvus* and total hardness and alkalinity in *C. cincinnatiensis* (Mackie and Flippance, 1983). Such data indicate that environmental influences on shell calcium content may extend well beyond simple phenotypic correlation with calcium availability.

While the proportion of $CaCO_3$ in the shell of *Ancylus fluviatilis* was not related to population growth rate, the actual weight of $CaCO_3$ in the shell of a standard individual was significantly related to growth rate such that individuals from faster growing populations had shells with a greater mineral weight than those from slower growing populations (Fig. 5). As there was no significant change in the proportions of $CaCO_3$ and protein in the shell with SL or growth rate, increase in shell mineral weight with increased growth rate implies a corresponding increase in shell organic content. The basis for this relationship between shell weight and growth rate in *A. fluviatilis* is unclear. However, if increased growth rates are associated with higher levels of primary productivity that allow relatively greater energy allocation to tissue and shell growth (Russell-Hunter, 1964, 1978; Aldridge, 1983; Burky, 1983; McMahon, 1983; Russell-Hunter and Buckley, 1983), faster growing individuals from energy rich microhabitats could be able to devote proportionately greater levels of energy to the fixation of both shell $CaCO_3$ and organic material, thus, producing thicker, more massive shells than individuals from energy poor habitats. As *A. fluviatilis* is a semelparous annual species, diversion of the majority of non-respired assimilated energy from shell production to tissue growth in food limited, slower growing populations can maximize reproductive effort by maximizing size at oviposition. In contrast, diversion of greater levels of energy to production of a more massive and stronger shell can increase chances of survival to reproduction and, thus, be selected for in more productive, less food limited habitats where individuals can sustain higher growth rates (Stearns, 1980).

A possible source of shell $CaCO_3$ variation which remains uninvestigated in freshwater molluscs is that of calcium content of ingested material. The digestive tract of freshwater pulmonates appears to be highly efficient in uptake of ingested Ca^{+2}, 95% of all ingested Ca^{+2} being absorbed from the gut in *Lymnaea stagnalis* Say (van der Borght and van Puymbroeck, 1966). Indeed, absorption of ingested Ca^{+2} has been shown to account for 20% of shell Ca^{+2} in *L. stagnalis* (van der Borght and van Puymbroeck, 1966). In other basommatophoran species, ingested Ca^{+2} makes up an equal to greater proportion of the shell mineral component dependent on water hardness. In water of low Ca^{+2} concentration ingested Ca^{+2} from a diet of lettuce accounted for 70.4% of shell Ca^{+2} in *L. peregra* and 78.8% in *P. corneus*. Even in a medium of high Ca^{+2} concentration ingested Ca^{+2} accounted for nearly 1/2 the shell Ca^{+2} at 45.6% in *L. peregra* and 46.0% in *Planorbarius corneus* (Young, 1975). As ingested Ca^{+2} can make up the major mineral component of the shell of freshwater gastropods, the Ca^{+2} content of periphyton or detritus on which they feed and even that of the substrata grazed can be more correlated with shell $CaCO_3$ content than ambient water Ca^{+2} concentration, particularly in softer waters where the contribution of ingested Ca^{+2} to the shell is greatest.

Certainly, increased food Ca^{+2} content has long been known to induce the production of heavier shells in land snails

(Oldham, 1929, 1934). As basommatophoran pulmonates evolved from a more terrestrial ancestral stock (McMahon, 1983), shell deposition of ingested Ca^{+2} can remain extremely important in shell formation and, therefore, be a major unaccounted, environmental, non-genetic source of what presently appears to be random genetically controlled interpopulation phenotypic variation in the shell $CaCO_3$ content of freshwater molluscs.

The sources of intraspecific, interpopulation variation in the shell morphometric ratios of freshwater molluscs have received extensive investigation. Early investigators considered shell shape to be rigidly genetically controlled and interpopulation variation the result of natural selection and adaptation to microenvironments (Mosley, 1935). Similar natural selection for shell shape in relation to relative degree of exposure to wave action and crab predation has been considered to account for interpopulation shell morphometric variation in isolated populations of the intertidal prosobranch gastropod, *Nucella lapillus* (L.) (Kitching *et al.*, 1966). However other investigators have indicated that environmental influences could induce a high degree of phenotypic plasticity in shell shape. Boycott (1938) showed that interpopulation differences in spire height disappeared when laboratory stocks of *Lymnaea peregra* from different populations were raised under the same conditions. Interpopulation differences in shell shape associated with degree of wave exposure in *N. lapillus* disappear when snails were reared under similar laboratory conditions (Crothers, 1977). Diver (1939) referred to such environmentally induced, non-genetic, interpopulation variability as "ecological plasticity" and there is extensive literature documenting such plasticity in freshwater molluscs (Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983, and references therein).

One source of non-genetic phenotypic variability in shell morphology lies in allometric change in shell shape as individuals become larger. Thus, in gastropods the ratios of aperture length to shell height (shell height corresponds to shell length in turbinate species), aperture width to shell height, and aperture length to aperture width will linearly vary with shell size (Vermeij, 1980). Such allometric variation in shell morphometric ratios is well documented in freshwater molluscs (Peters, 1938; Nickerson, 1972; Durrant, 1975, 1980; Hunter, 1975). In Irish *Ancylus fluviatilus* the AL/SH and AW/SH ratios declined with increasing aperture length and the AL/AW ratio increased with increasing aperture length both within and across populations (Fig. 3). Thus, larger individuals tended to have steeper shells with narrower apertures. A similar negative allometry of the AL/SH and AW/SH ratios with increasing aperture length has been reported for British *A. fluviatilis*. However, in contrast to our results, the AL/AW ratio was isometric with shell length (Sutcliff and Durrant, 1977). Only the AL/SH ratio declines with increasing AL in the North American stream limpet, *Ferrissia rivularis,* while the ratios of AW/SH and AL/AW are isometric with aperture length (Nickerson, 1972). In *Stagnicola elodes* both the SL/AL and SL/AW ratios increase as individuals grow larger, but the AL/AW ratio remains constant (Hunter, 1975).

As freshwater pulmonates generally display annual life cycles in which adults die soon after spring reproduction (Russell-Hunter, 1961a, 1961b, 1964, 1978), the mean population shell length, and, therefore, the mean shell morphometric ratios of a population can exhibit considerable annual variation. Thus, all interpopulation comparisons of shell morphometric ratios should be based on ratios of standard sized individuals estimated from regressions of linear shell dimensions or morphometric ratios on shell length (Peters, 1938; Nickerson, 1972; Hunter, 1975; Durrant, 1975, 1980; Sutcliff and Durrant, 1977) or on size adjusted means computed from the analysis of covariance of regressions relating shell morphometric parameters for each populations (Zar, 1974).

In both *Ferrissia rivularis* (Nickerson, 1972) and *Stagnicola elodes* (Hunter, 1975) the shape of the aperture (defined by the AL/AW ratio) is reported to be isometric with shell growth. While the level of increase in the AL/AW ratio with shell growth is less than that of the decrease in AL/SH and AW/SH in *Ancylus fluviatilis*, it proved highly significant both within and between samples (Fig. 3, Table 3). Lack of allometric variation in the AL/AW ratio with AL in *F. rivularis* and *S. elodes* led both investigators to conclude that aperture shape was rigidly genetically controlled in these species, and that interpopulation variation in the AL/AW ratio was a result of gene pool differences between populations. In contrast, the shell steepness indices of AL/SH (or SL) and AW/SH (or SL) allometrically varied with the mean shell size of the population and, therefore, variation in these ratios was considered to be a result of non-genetic, environmentally induced plasticity associated with trophic conditions controlling mean population shell size (Nickerson, 1972; Hunter, 1975). Further evidence for the genetic control of aperture shape in these species was provided by reciprocal transfer experiments, whereby newly hatched juvenile snails were transferred between populations and raised in cages along with caged control individuals from the recipient population. Such transfer experiments showed that while the AL/SH and AW/SH ratios, reflecting shell steepness of transferred individuals, approached those of the control recipient populations indicating environmental influence, the aperture shape index (AL/AW) remained similar to that of the source population from which individuals were transferred indicating a relatively rigid genetic control of this morphometric feature (Nickerson, 1972; Hunter, 1975).

Our data do not support a hypothesis of such rigid genetic control of aperture shape in *Ancylus fluviatilis*, instead it appears to be allometric with shell growth rate. Vermeij (1980) has suggested that the allometry of shell morphometrics in molluscs can be highly correlated with growth rate. To date no studies have attempted to correlate the interpopulation variation in the shell morphometrics of freshwater molluscs with interpopulation variation in their growth rates. When the shell shape ratios of AL/SH, AW/SH and AL/AW were estimated for a standard sized individual of *A. fluviatilis* from the appropriate regressions of individual ratios versus AL for each collected population, ratios of AW/SH and AL/AW were found to be significantly correlated with the estimated mean annual shell growth rate (Figs. 6 and

7, Table 4). In addition, lack of significant correlation of the AL/SH ratio to growth rate was found to result from the allometric reduction of relative AL in fast growing populations.

There is extensive evidence that interpopulation variation in growth rates of freshwater gastropods results almost entirely from variations in environmental primary productivity (in terms of food quality and quantity) with faster growing individuals occurring in environments with greater standing crop biomass of periphyton or detritus and/or food sources with higher protein contents (Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983; McMahon *et al.*, 1974; and references therein). For almost all gastropod species tested, reciprocal transferral of individuals from one population to another resulted in transferred individuals growing at rates equivalent to that of the recipient population (Hunter, 1975; Eversole, 1978; Payne, 1979; Aldridge, 1982) including the ancylid limpets, *Ferrissia rivularis* (Burky, 1971; Nickerson, 1972; Romano, 1980) and *Laevapex fuscus* (McMahon, 1975). McMahon *et al.* (1974) demonstrated that the protein content of ingested periphyton was directly correlated with population growth rates in *Stagnicola elodes* and the ancylid limpet, *L. fuscus*. Annual variations in mean population shell growth rates of *Ancylus fluviatilis* and three other freshwater gastropod species were found to be correlated with both average hours of sunshine and average ambient temperature during the growth period (Russell-Hunter, 1953, 1961a), both directly related to primary productivity. Indeed, carefully controlled reciprocal transfer and laboratory rearing experiments have demonstrated that the majority of interpopulation variation in population dynamics, life history tactics and bioenergetics of freshwater gastropods appears to be environmentally induced rather than the result of genotypic differences between populations (Burky, 1971; Nickerson, 1972; Hunter, 1975; McMahon, 1975; Eversole, 1978; Brown, 1979, 1983, 1985a, 1985b; Payne, 1979; Romano, 1980; Aldridge, 1982). As such, the three fold interpopulation variation in estimated annual shell growth rate for Irish populations of *A. fluviatilis* does not appear to reflect genetic differences, but, rather, environmental differences in the primary productivity of their respective environments. Certainly, the highest growth rates were recorded in populations from larger rivers on the eastern coast or in the midlands of Ireland (sites 43, 44, 45, and 48; Fig. 1, Table 2) which were far more productive than small oligotrophic streams and ponds sampled in Counties Galway and Donegal (sites 1-39, Fig. 1, Table 2).

A similar allometry between shell morphology and shell growth rate has been reported for the marine intertidal littorine snail, *Littorina littorea* (L.) in which faster growing individuals from habitats of higher food availability produced shells of relatively greater globosity (i.e., shell width : shell length ratio increased with increased growth rate) (Kemp and Bertness, 1984) which corresponds directly to the increase in the AW/SH ratio observed in faster growing specimens of *Ancylus fluviatilis*. However, faster growing individuals of *L. littorea* also produced relatively lighter shells (Kemp and Bertness, 1984), unlike *A. fluviatilis* in which faster growing populations were characterized by shells with greater relative weights (Fig. 5). Such interspecific differences indicate that growth rate allometries of shell morphometrics in molluscs are probably species specific and like allometries with size (Vermeij, 1980) cannot be generalized for the entire phyletic group.

That interpopulation variation in growth rate exhibited a strong positive correlation with mean population AL/SH ratios and a strong negative correlation with mean population AL/AW ratios indicated that the majority of such variation in *Ancylus fluviatilis* is environmentally induced via the effects of environmental productivity on population growth and mean adult shell length. Therefore, individuals of standard size from fast growing populations tend to have more depressed shells with rounder apertures than those from slower growing populations (Figs. 4, 6).

The influence of environment on shell shape is highly apparent when shell morphometric ratios are compared between individuals taken from upstream and downstream locations in rivers with continuous populations or from the same site in different years. For Irish *Ancylus fluviatilis* the means of all three ratios were found to vary significantly in samples of one of two populations collected at upstream and downstream sites (Table 5), while both mean AL/SH and AW/SH varied significantly between three of six populations sampled in 1982 and 1984 (Table 6). One of six populations sampled in 1982 and 1984 displayed significant variation in the mean AL/AW ratio (Table 6). If any of these three shell morphometric ratios were under rigid genetic control and, therefore, minimally affected by environmental influences, such intrapopulation variation in shell morphometrics would not be expected. It would require the existence of small, discrete, highly genetically isolated populations within single stream or river systems or for individuals and populations to be subject to exceptionally high levels of geographical isolation, natural selection and evolution, respectively. Instead, environmental influences affecting shell shape offer a much more plausible explanation for such variation. Indeed, growth rates have been shown to vary widely in populations of *A. fluviatilis* from the same river system (Maitland, 1965; Durrant, 1975, 1977) and in a single population from year to year depending on annual climatic conditions (Russell-Hunter, 1953, 1961a). Our data indicate that such environmentally induced variation in growth rate would lead to variation in shell morphometrics. However, growth rates varied little in populations of *A. fluviatilis* exhibiting significant shell shape variation across years (Table 2) indicating that environmental influences other than those which alter growth rates can also affect shell morphology.

The apparent allometry of shell shape with growth rate does explain the variation in shell shape reported for *Ancylus fluviatilis* in relation to water flow. Specimens of *A. fluviatilis* from areas of rivers with higher current flow rates are reported to have both steeper shells marked by higher AL/SH and AW/SH ratios with narrower apertures marked by reduced AL/AW ratios compared to those from lower flow areas of the same river (Durrant, 1975). Similarly, specimens of *A. fluviatilis* from impoundments or lentic habitats have flatter shells with rounder apertures than those from lotic habitats (Durrant, 1975, 1977, 1980; Sutcliff and Durrant, 1977). It has been

suggested that the steeper shells of lotic individuals are a result of the continuous downward pull of pedal musculature required to maintain attachment in high current flows (Durrant, 1975) or due to differences in the allometric relationship of shell height to aperture width, whereby height increases relative to width at a higher rate in individuals from lotic habitats, as a result of selection for a more streamlined shell, less resistant to the effects of current (Sutcliff and Durrant, 1977). The mean population AL and growth rates of *A. fluviatilis* from more lentic habitats are generally greater than those from lotic habitats (Russell-Hunter, 1953, 1961a, 1961b, 1964; Geldiay, 1956; Maitland, 1965; Durrant, 1975, 1977). This difference in growth rate has been directly attributed to the greater primary productivity of lentic or low flow rate lotic habitats compared to high flow rate lotic habitats (Geldiay, 1956; Russell-Hunter, 1961a, 1961b; Maitland, 1965). The results presented here suggest this sort of shell shape variation between individuals from lentic and lotic habitats is more simply explained by the allometry of shell shape with growth rate whereby faster growing individuals from more productive lentic or low flow habitats characteristically have less steep shells with rounder apertures of greater relative area than do individuals with slower growth rates from less productive high flow lotic habitats (Figs. 6, 7, Table 4).

CONCLUSIONS

While this report has been primarily concerned with the variation in shell morphometrics of *Ancylus fluviatilis,* it also has focused on a major topic in the ecology of freshwater molluscs, the source of their extensive intraspecific interpopulation variation. Such variation exists not only in shell morphology and $CaCO_3$ content, but also in many other aspects of their biology including growth, reproduction, population dynamics, life history traits, physiological responses and bioenergetic budgeting (see Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983; for reviews of intraspecific interpopulation variation in freshwater molluscs). In many such studies variations between populations are assumed to result strictly from genetic differences to which an adaptive significance is assigned *a posteriori* to explain the natural selection pressures leading to such variation. Diver (1939) was among the first to point out that the majority of seemingly genetically controlled interpopulation variation in molluscs may actually be non-genetic phenotypic plasticity (ecological plasticity) in response to subtle environmental variation. Stearns (1980) has recently suggested that developmental and physiological plasticity can explain the majority of interpopulation variation in life history traits. Indeed, environmental, non-genetic influences have been shown to be the major cause of interpopulation differences in shell morphology as rearing under constant laboratory conditions caused phenotypic differences to disappear in the marine species, *Nucella emarginata* (Deshayes) (Palmer, 1985) and *N. lapillus* (Crothers, 1977) and the freshwater pulmonate, *Lymnaea stagnalis* (L.) (Arthur, 1982).

Attempts to assign an adaptive significance to such variation could lead to incorrect and rather anomalous hypotheses regarding the evolution of these traits. This can be particularly true of the utilization of shell morphological variation in the interpretation of molluscan fossil records. If shell growth rate has a significant impact on molluscan shell morphology, as it does in *Ancylus fluviatilis,* any major environmental perturbations effecting shell growth such as changes in annual average temperature, water level, calcium availability and/or primary production could induce profound and immediate changes in a species' shell morphology synchronously over a wide geographic area. The Pleistocene fossil records of 12 species of land snails were characterized by variations in shell size, growth rate, mass and morphology that were clearly associated with climatic change during glacial periods and, therefore, a result of environmentally induced ecophentypic plasticity (Gould, 1970). In the past, such apparently rapid and synchronous changes in the shell morphology of fossil gastropods have been attributed to rapid or "punctuated" allopatric speciation (Eldredge and Gould, 1972; Williamson, 1981). However, if environmental change directly effects shell growth rate, major non-genetic, growth related allometric changes in the shell morphology of molluscan fossil lineages could be misinterpreted as speciation events. Thus, apparent punctuated speciation events marked by relatively rapid change in the shell morphology of a molluscan fossil lineage could, in reality, result from geological or climatic episodes that either inhibit or stimulate shell growth rates (for examples see Gould, 1969a, 1969b, 1971; Eldredge and Gould, 1972) or from changes in food availability associated with changes in lake level (Williamson, 1981). Certainly, growth related ecophenotypic variation could be the source of the punctuated changes in shell morphology reported to occur simultaneously in 13 different molluscan lineages during major lake level transgression-regression episodes in a fossil assemblage from the Turkana Basin (Williamson, 1981), particularly as such major shell morphological changes were associated with "stunting" of shell size (an indication of reduced growth rates) and as new morphotypes appeared in very large populations (Williamson, 1981) resistant to rapid allopatric speciation (Eldredge and Gould, 1972; Gould and Eldredge, 1977). In this assemblage even the parthenogenic species, *Melanoides tuberculata* (Müller), which should not respond rapidly to selective pressures, displayed major variations in shell morphology. In addition, all lineages returned abruptly to ancestral morphology during periods of relative environmental stability (Williamson, 1981). In light of the data presented for *A. fluviatilis*, it is possible that such rapid and simultaneous changes in shell morphology could be explained by non-genetic, allometric mechanisms associated with major changes in population growth rates induced by episodes of environmental stress and/or instability.

Our own research has shown that the majority of interpopulation variation in the shell calcium content and shell shape of *Ancylus fluviatilis* appears to be a result of such phenotypic plasticity, eliminating the necessity of invoking genetically based explanations involving founder effects,

genetic drift and/or natural selection. The basis of such interpopulation variation can only be rigorously approached by the development of hypotheses which either carefully consider the possible environmental and allometric causes for such variation, through the utilization of reciprocal transfer of individuals between populations, or by the rearing of individuals from different populations in the laboratory through several generations (McMahon and Burky, 1985). While such carefully controlled *a priori* approaches have revealed hard evidence for isolated cases of genetically based physiological race formation in freshwater molluscs (Forbes and Crampton, 1942; McMahon, 1975, 1976; McMahon and Payne, 1980; Russell-Hunter *et al.*, 1981), the vast majority of such studies, too numerous to cite here (see Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983, for reviews of the sources of interpopulation variation in freshwater molluscs) have indicated that almost all observed interpopulation variation is the result of environmentally induced phenotypic plasticity. In this regard, Brown (1983, 1985a) in careful reciprocal transfer experiments has demonstrated that the vast majority of interpopulation variation in the life history traits of populations of *Stagnicola elodes,* previously assumed to be the result of natural selection and genotype differentiation, instead resulted from environmental differences in productivity and ambient temperature. Interpopulation variation in the shell morphometrics of *Sphaerium striatinum* has been shown to be much more extensive than isozyme variation (Hornbach *et al.*, (1980) or whole body protein variation in the freshwater pulmonate, *Radix quadrasi* (Bequaert and Clench) (Pagulayan and Enriquez, 1983). Such results imply that the majority of interpopulation shell morphological variation in these species is accounted for by non-genetic environmental factors. Even the frequency distributions of isozymes of lactate dehydrogenase are reported to display extensive annual, environmentally induced variation in *Cepaea nemoralis* (L.) (Gill, 1978). Certainly, the extensive capacity of freshwater molluscs for variation in response to environmental perturbation ultimately has a genetic basis and is subject to natural selection. For many species of freshwater molluscs which inhabit temporally unstable, highly variable habitats (Russell-Hunter, 1964, 1978, 1983; McMahon, 1983) the evolved ability of individuals to compensate or adjust major aspects of their morphology, growth, reproduction, life history traits and physiological responses to a wide range of both short and long term environmental variations is highly adaptive. Such phenotypic plasticity allows species such as basommatophoran snails to successfully invade and inhabit marginal, highly variable, temporally unstable shallow freshwater habitats (Russell-Hunter, 1961a, 1961b, 1964, 1978, 1983; Nickerson, 1972; Brown, 1983, 1985a, 1985b; McMahon, 1983).

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